A METHOD FOR ANALYSIS OF PLANT COMPETITION EXPERIMENTS

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ABSTRACT

A method is outlined for estimating the competitive ability of one species over another, grown in pure and mixed culture, to fixed treatments factorially applied. An application of the method to assess the response of two grasses to increasing levels of substrate phosphorus and nitrogen is described.

INTRODUCTION

Experiments designed to estimate the competitive ability of one species over one of a number of other species are an important extension of field studies in ecology. The method presented outlines the analysis of such an experiment for two species grown in pots, both singly (pure culture) and in competition (mixed culture). The competitive advantage of one species over another (assessed in terms of biomass or any other attribute) depends upon a number of factors, a selection of which can be tested experimentally, each at a number of levels. Such a factorial experiment, sufficiently replicated and laid out in randomized blocks can be statistically analysed by analysis of variance for both pure and mixed cultures. By weighting the results inversely as their variances, the data can be combined to provide estimates of the responses to the fixed treatments factorially applied, in terms of competition between the two species.

The method was applied to a grassland ecology problem being studied at the Plant Industry Division, C.S.I.R.O., Canberra, following the method of E.J. Williams (1962), and results of the analyses of variance and tables of means for the competitive effect assessed by this method, are given.

METHOD OF ANALYSIS

The experimental error variances arising from comparisons of data between species grown singly (in pure culture), between totals from mixed culture pots, and within mixed culture pots can be designated s, c_1 and c_2 respectively. Since the variances c_1 and c_2 are on a half pot basis and s is the variance of halved whole pot data it might be assumed that $c_1 = 2s$, but if plants of different species compete in a different way from plants of the same species there would be a departure from this relationship. Therefore it is better to use the ratio c_1/s estimated from the experimental data to weight the combined results which measure the competitive effect.

TABLE 1. RESULTS OF ANALYSIS OF VARIANCE FOR LOG (YIELD/HALF POT) OF PURE AND MIXED CULTURES SEPARATE AND COMBINED $(X_{12} + X_{21}) - (X_{11} + X_{22})$

		Pure culture		Mixed culture		Combined analysis pure and mixed cultures			
Source of variation	*df*	*MS*	*Fs*	*MS*	*Fs*	*Source of variation*	*df*	*MS*	*Fs*
Replicates	4	0.00480	2.5*	0.01615	2.1*ns*				
Nitrogen N	2	0.57140	302.6***	0.39443	51.7***				
Phosphorus P	2	0.18933	100.3***	0.17906	23.4***				
N.P interaction	4	0.07766	41.1***	0.06104	8.0***				
Species	1	0.02813	14.9***	3.99618	138.1***	Pure vs. Mixed (P vs. M)	1	0.69666	91.2***
N.Species	2	0.00136	*ns*	0.09408	3.2*	N.(P vs. M)	2	0.01410	1.8*ns*
P.Species	2	0.00729	3.9*	1.14650	39.6***	P.(P vs. M)	2	0.15776	20.7***
N.P.Species	4	0.00069	*ns*	0.05593	1.9*ns*	N.P.(P vs. M)	4	0.01200	1.6*ns*
Error S	68	0.00189	C_1	0.00764	(32 *df*)	Error C_1	32	0.00764	
			C_2	0.01891	(32 *df*)	$W = C_1/S = 4.04$			

df = degrees of freedom

MS = mean square

Fs = variance ratio

levels of significance, α

ns = not significant

* = 0.05

** = 0.01

*** = 0.001

The results for each half pot can be represented as follows:

Species 1 grown alone	x_{11}
Species 1 grown with species 2	x_{12}
Species 2 grown with species 1	x_{21}
Species 2 grown alone	x_{22}

A significant departure of $(x_{12} + x_{21}) - (x_{11} + x_{22})$ from zero indicates competition between the species, and the interaction of this contrast with the factors under study leads to variance ratio tests of the main effects and interactions of the factors, on the competition of the two species. While the analysis of the pure cultures of the two species should be treated as a fully factorial design with a single error S, the mixed culture analysis must be analysed as for a split-plot design with the two error terms C_1 and C_2. Although the C_1 error is affected by systematic differences between pots which do not affect the C_2 error, competition effects may result in C_2 being appreciably larger than C_1.

The combined analysis of variance (Table 1) for the comparison of pure and mixed cultures uses the difference $(x_{12} + x_{21}) - (x_{11} + x_{22})$ as the variable measuring competition. It combines the error variances from between mixed culture pots (C_1 error) and between pure culture pots (S error) in an inverse weighting factor for the sums of squares which is

$$1/rp(p - 1)\{C_1 + (p - 1)S\} = w/\{rp(p - 1)(p + g)\}$$

where $w = C_1/S$
$g = w - 1$
p = number of species
r = number of replicates

The basic variance for the combined analysis is C_1 and the weighted sums of squares for the treatment effects and the overall contrast of pure and mixed pot totals are tested against C_1.

The results of an experiment (Table 2) are expressed as the mean values over the r replicates of differences $(x_{12} + x_{21}) - (x_{11} + x_{22})$ for all the factorial combinations and the main effects of each factor. Least significant differences (*L.S.D.*) are derived from the C_1 error weighted by $[p(p - 1)(p + g)/wr]$. The degrees of freedom (df) for this weighted C_1 can be approximated by a method of Satterthwaite (1946),

$$f' = \frac{[C_1 + (p - 1)S]^2}{\frac{C_1^2}{f_1} + \frac{S^2}{f_2}} \qquad \text{where } f_1 = df \text{ for } C_1,\quad f_2 = df \text{ for } S$$

and the t values used for the *L.S.D.* for comparing the means are based on f' degrees of freedom.

$$L.S.D. = t_{\alpha[f']} \quad \sqrt{2C_1\, p(p - 1)(p + g)/wrn}$$

where α = 0.05, 0.01 and 0.001
n = sample size.

TABLE 2. MEANS FROM 5 REPLICATES OF DIFFERENCES BETWEEN MIXED AND PURE CULTURE TOTALS OF LOG(YIELD/HALF POT) FOR THE N.P FACTORIAL EXPERIMENT WITH POA LABILLARDIERI AND THEMEDA AUSTRALIS

	Levels of N			
Levels of P	N_0	N_1	N_2	P means
P_0	0.087	0.004	0.072	0.055
P_1	0.241	0.431	0.448	0.373
P_2	0.096	0.218	0.172	0.162
N means	0.141	0.218	0.231	0.197

Least significant differences weighted by $\sqrt{\{p(p-1)(p+q)\}/wr}$

$f' = 48$ degrees of freedom

Significance levels	N, P main effects	P at each level of N N at each level of P
5.0%	0.101	0.175
1.0%	0.135	0.234
0.1%	0.177	0.306

APPLICATION OF THE METHOD

The method was used in the analysis of a pot experiment (Groves et al 1973) to assess the response of *Themeda australis* and *Poa labillardieri* to increasing levels of substrate phosphorus and nitrogen. The ability of *Poa* plants to absorb nutrients and grow in response to a low level of added phosphorus (especially in the presence of nitrogen) at the expense of *Themeda* plants is similar to their response in the field in southern New South Wales. *T. australis* is a dominant grass over much of the Upper Shoalhaven Valley, while *P. labillardieri*, also indigenous, becomes dominant over extensive areas and assumes the characteristics of a weed when these areas are 'developed' for intensive sheep grazing with applications of superphosphate and a gradual increase in soil nitrogen level as legumes become more abundant.

The analysis of variance (Table 1) for the pure culture pots shows that, while there is a very marked response by both species to increasing amounts of nitrogen and phosphorus, *P. labillardieri* has a greater ability to make use of phosphorus than *T. australis*. For the mixed culture analysis, the variance ratio test for this differential response is greater by tenfold, as is the overall superiority of *P. labillardieri* under conditions of competition with *T. australis*. It is not surprising therefore that, in the combined analysis, this marked difference between mixed and pure cultures is shown to be very highly significant and that there is a much greater response to phosphorus, particularly in the presence of nitrogen. Competition for low amounts of added phosphorus (Table 2) is the most intense; almost significantly so in the absence of nitrogen, with a very high level of significance with low nitrogen addition, while the slight extra response to low phosphorus with the addition of an extra amount of nitrogen is certainly non-significant. Competition for phosphorus is very significantly reduced at higher levels of phosphorus and only remains significantly higher than for no phosphorus at the low level of nitrogen. The minimal competition effect with low nitrogen, no phosphorus is worth noting.

ACKNOWLEDGMENTS

I wish to thank R.H. Groves, Plant Industry Division, C.S.I.R.O., who provided the experimental data. The work was undertaken for the Division of Mathematical Statistics C.S.I.R.O., Canberra.

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